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GLOBAL CHANGE BIOLOGY

Contrasting effects of climate on juvenile body size in a Southern-hemisphere passerine bird

Running head: Contrasting effects of climate on body size

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Abstract

Despite extensive research on the topic, it has been difficult to reach general conclusions as to the effects of climate change on morphology in wild animals: in particular, the effects of warming temperatures have been associated with increases, decreases or stasis in body size in different populations. Here, we use a fine-scale analysis of associations between weather and offspring body size in a long-term study of a wild passerine bird, the cooperatively-breeding superb fairy-wren, in south-eastern Australia to show that such variation in the direction of associations occurs even within a population. Over the past 26 years, our study population has experienced increased temperatures, increased frequency of heatwaves, and reduced rainfall – but the mean body mass of chicks has not changed. Despite the apparent stasis, mass was associated with weather across the previous year, but in multiple counteracting ways. Firstly, (i) extremely-recent heatwaves were associated with reduced chick mass, but there also positive associations of (ii) higher maximum temperatures and (iii) higher rainfall, both occurring in a period prior to and during the nesting period, and finally (iv) a longer-term negative association with higher maximum temperatures following the previous breeding season. Our results illustrate how a morphological trait may be affected by both short- and long-term effects of the same weather variable at multiple times of the year, and that these effects may act in different directions. We also show that climate within the relevant time windows may not be changing in the same way, such that overall long-term temporal trends in mean body size may be minimal. Such complexity means that analytical approaches that search for a single ‘best’ window for one particular weather variable may miss other relevant information, and is also likely to make analyses of phenotypic plasticity and prediction of longer term population dynamics difficult.

Introduction

Understanding and anticipating the effects of ongoing climate change on natural populations is now a priority for environmental science. A number of studies of different animal and plant species have documented temporal trends in population size, or in the average values of characteristics such as phenology (timing), suggesting rapid responses to recent climate change (Fitter & Fitter, 2002; Parmesan, 2006; Thackeray *et al.*, 2010). However, the effects of a changing climate may vary between populations, between climatic variables, and between different times of the year. The latter point is especially relevant for long-lived species with complex life histories, for which different times of the year may involve different effects of weather. In extreme cases, a shift towards warmer temperatures at one time of year may have entirely different implications than a shift towards warmer temperatures at other times of year (Cook *et al.*, 2012). Here, we illustrate exactly this scenario in an animal population, and show that offspring body size in a wild bird is associated in contrasting ways with short-term versus long-term effects of temperature.

An animal's body size may be a key predictor of its fitness, frequently determining both its survival and its fecundity (Blanckenhorn, 2000; Kingsolver & Huey, 2008). However, despite the fundamental importance of size for individual fitness, and hence for population dynamics, how climatic factors drive body size variation remains poorly understood. Observations that reductions in body size of many organisms are correlated with rising temperatures have been interpreted as adaptive changes in accordance with Bergmann's rule (Gardner *et al.*, 2009; Gardner *et al.*, 2011; Salewski *et al.*, 2010; Yom-Tov, 2001) – whereby a mean increase in body size with increasing latitude is seen as an adaptive response to colder climates (Bergmann, 1847; Meiri, 2011). However, to date there is little explicit evidence that observed changes are indeed adaptive microevolution due to genetic change (Husby *et al.*,

2011; Teplitsky *et al.*, 2008), rather than simply a phenotypically plastic response to changing availability of resources (Gienapp *et al.*, 2008). Furthermore, declines in body size are by no means universal (Gardner *et al.*, 2014a; Gardner *et al.*, 2011; Meiri *et al.*, 2009; Yom-Tov & Geffen, 2011); other studies have reported increases in size, and/or positive temperature-size correlations, and these in turn have frequently been interpreted as evidence of climate-driven changes in primary productivity that affect food or food quality (Gardner *et al.*, 2014b; Gardner *et al.*, 2011; Gienapp *et al.*, 2008; Ozgul *et al.*, 2010; Teplitsky *et al.*, 2008; Yom-Tov & Geffen, 2011). Such diversity between populations in the direction of associations makes it difficult to generalise as to the effects of climate change on morphology. However the different scenarios all point to an important role of phenotypic plasticity in determining trends in body size, an understanding of which requires knowledge of which aspects of a changing climate are most influential.

Long-term, individual-based studies of wild animal populations are valuable tools with which to explore associations between weather variables and biological traits of interest (Clutton-Brock & Sheldon, 2010; Gienapp & Brommer, 2014; Visser, 2008). Whilst such studies obviously cannot explicitly test causal explanations for such associations, due to their observational nature, they allow correction for other potentially important sources of between-individual variation, for example those due to ontogenetic, demographic or spatial variation (e.g. Ozgul *et al.*, 2010; Ozgul *et al.*, 2009; Stopher *et al.*, 2014; van de Pol *et al.*, 2011). The extensive variability in magnitude and direction of trends in body size reported across different studies also argues strongly for substantial sample sizes, both in terms of number of years sampled and number of individuals per year, with which to ensure robust estimation of trends (Meiri *et al.*, 2009; Yom-Tov & Geffen, 2011). Large-scale long-term

studies over several decades therefore become especially valuable for exploring climate-trait associations.

To date, birds in general – and passerines in particular – have been relatively well-represented in the study of effects of climate change (Møller *et al.*, 2010), due in part to the availability of several impressive long-term data-sets in Northern Europe or North America (see for example review in Gienapp & Brommer, 2014). However, several fundamental gaps remain. In particular, Southern Hemisphere populations, species and habitats are generally under-represented in such work: for example, they comprise less than 4% of the number of bird species given in Gardner *et al.*'s (2011) extensive review of trends in body size. The imbalance reflects a strong northern-temperate bias, and hence geographically unbalanced research effort, in avian studies (Ducatez & Lefebvre, 2014). Furthermore, studies of associations between weather and performance in non-migratory bird species have typically focused on immediate effects of recent weather, presumably under the assumption that substantial lags between environmental cues and the timing of key events are unlikely (though see Gardner *et al.*, 2014b). This focus is in contrast both to studies of migratory bird species (e.g. Norris & Taylor, 2006; Pasinelli *et al.*, 2011; Saino *et al.*, 2004), and also to studies of mammals where, particularly for larger species, long gestation periods may be expected to generate associations between weather at a given time and the observed phenotypes of offspring born much later (e.g. Burthe *et al.*, 2011; Stopher *et al.*, 2014). Finally, the majority of research to date on the effects of climate change in natural systems (on any taxa) has focused on effects of increasing temperatures (e.g. Thackeray *et al.*, 2010), with relatively less attention paid to effects of concurrent changes in precipitation (e.g. Lane *et al.*, 2012), or to manifestations of extreme events such as heatwaves (e.g. Cunningham *et al.*, 2013a; du Plessis *et al.*, 2012; Gardner *et al.*, 2014b).

We present data from a 26-year individual-based study of an Australian cooperatively breeding passerine, the superb fairy-wren (*Malurus cyaneus*). Our aim was to identify the timing and nature of any effects of climate on chick mass, a trait that we know to be under strong positive directional viability selection (for recruitment to the breeding population, the standardized linear selection gradient is 0.263 (0.048 SE); LK and AC, unpubl. results). Over the study period of 1988-2013, weather at our study site in south-eastern Australia has shown a distinct change towards hotter maximum temperatures, an increased frequency of heatwaves, and (with the exception of a single very wet year in 2010) lower rainfall (Figure 1a-c; see figure legend for statistical details). In contrast, chick body size, as assessed by mass, did not change over this period (Figure 1d). The most parsimonious explanation for such stasis would be insensitivity to climatic variation. However any such lack of sensitivity would be in contrast to recent evidence from the same population for effects of weather both on the phenology of male plumage moult (van de Pol *et al.*, 2011) and on breeding success (Cockburn *et al.*, 2008a). Here, we explore these contrasting results.

Materials and Methods

Superb fairy-wren study population

We used data from the breeding seasons of 1988 through to 2013 (ending in February 2014) from the long-term study of a population of superb fairy-wrens (*Malurus cyaneus*) in the Australian National Botanic Gardens, Canberra (35°16'S, 149°6'E) (Cockburn *et al.*, 2003). Fairy-wrens are cooperative breeders: a territory held by a breeding pair may contain as many as four or even five additional males, all of whom help rear offspring (Cockburn *et al.*,

2008b). Females may raise up to three broods to independence each year; unlike the great majority of species used in equivalent studies of passerine birds, superb fairy-wrens are not nestbox breeders and so high rates of nest predation may result in a female laying as many as eight or nine clutches per season (Cockburn *et al.*, 2008b).

The study population's breeding season runs from approximately October to February, peaking in early December (SI Fig. S1). Chicks were weighed and banded in the nest between the ages of 5 to 8 days (the entire nesting period lasts 11 to 13 days, but chicks were not measured after 8 days to avoid the risk of premature fledging). Data were available for a total of 6405 chicks from 2309 nests (mean \pm SD = 7.07 ± 1.04 g; observations of mass <4g were excluded as probably representing severe pathology; these formed 0.3% of the original sample). The total study period comprised two sub-periods: an initial sub-period that involved a smaller section of the study area and involved the breeding seasons of 1988-1991, and then the main period consisting of more extensive study across an expanded area, which began in 1992. In addition to an approximately two-fold increase between sub-periods in the number of territories involved, there was also a change in the time of chick measurement from late afternoon to early morning; given the rapid rates of daily growth in chicks shown below, this affected measurements of chick mass. We therefore included 'sub-period' as a two-level factor in all models presented below (but we also repeated all analyses using data from only 1992 onwards, and found effectively identical results, which we do not present separately here.)

Weather data

Data on the daily weather at Canberra airport (~8 km east of the study area) were obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/data>). For ease of comparison across the literature, we focussed on the readily-interpretable variables of daily *maximum temperature*, MaxT (mean=20.3°C across the study period), and precipitation (referred to henceforth as *rainfall*, although it will necessarily also include the very rare occasions of snow or hail; mean annual rainfall=585.9mm across the study period). Comparisons of models with either maximum or minimum temperature returned highly congruent results for identification of relevant time windows, but indicated stronger effects of the former. Finally, given that effects of temperature may be non-linear, and in particular that there may be additional effects at extreme temperatures, we also tested for effects of ‘*heatwaves*’, defined as maximum temperature over 35°C on a particular day (following Cunningham *et al.*, 2013b). 35°C was chosen following preliminary analyses, in which we compared threshold values of several temperatures using the modelling procedure described below, and 35°C emerged as the most informative threshold (average number of heatwaves per year = 6.68).

Statistical analyses

We used linear mixed models (Zuur *et al.*, 2009) to analyse variation in chick mass; all analyses were run in R version 3.0.2 using the library “lmerTest” (R Development Core Team, 2015). All models contained two random effects: *Cohort*, to account for the multiple measurements in each year, which ran through to February of the subsequent calendar year (e.g. Cohort 1991 contains all nests between September 1991 and February 1992); and *Brood* identity, to account for the multiple chicks within a brood (note that this component of

variance will also contain any variance due to additive genetic and maternal effects not accounted for by the fixed effects; Kruuk & Hadfield, 2007). Fixed effects (described below) were evaluated using models fitted with maximum likelihood rather than REML, as REML will be affected by the scaling of fixed effects (Zuur *et al.*, 2009).

Initial model

Because we also needed to account for the multiple other variables likely to affect chick mass, we first constructed a linear mixed model of chick mass without any weather variables but containing the following fixed effects:

Chick age (days): Fitted as a continuous variable ranging from 5-8 days, with a quadratic term to account for non-linearity.

Chick sex: Chick sex was determined genetically for the majority of individuals (as chicks cannot be sexed phenotypically in the nest). Sex was unknown for chicks for which we do not yet have genotypic data, and so Sex was necessarily fitted as a three-level factor: female (38.7%), male (43.3%), and unknown (17.9%). (The higher percentage of males is due to male philopatry, which generates a higher probability that a male will have been observed later in life and thereby sexed phenotypically.)

Brood size: the number of chicks in the nest at the time of measurement, ranging from 1 to 5, with a mode of 3 (57% of nests).

Study sub-period – a two-level factor for the two periods of 1988-1991 vs 1992-2013 (see above).

The covariates chick age and brood size were mean-centred prior to analysis. Before investigating associations with different weather variables, we first tested for any temporal trend in chick mass by adding year as a covariate to the initial model. Then, for each weather

variable in turn (heatwaves, maximum temperature and rainfall), we compared models adding different time windows (see below) to the initial model (i.e. excluding year).

Identifying time windows

(i) Identifying time windows for each weather variable

To find the key weather variables determining trait expression, we used a ‘sliding window’ approach (Brommer *et al.*, 2008; Estrella *et al.*, 2007; Husby *et al.*, 2010; Phillimore *et al.*, 2012). This involved estimating an index defined for a given time window as either (i) for heatwaves, whether or not the mean MaxT across the window exceeded 35°C (a binary variable, 0/1); (ii) for MaxT, the mean MaxT across the window; or (iii) for rainfall, the sum of the total rainfall across the window. For each of these three weather indices in turn, we then compared the strength of their associations with chick mass in linear mixed models, including the fixed and random effects described above, across different windows. The start date and duration (width) of the window was varied in increments of days; the consequent strength of statistical support for that model was then evaluated using the Akaike Information Criterion (AIC). Each linear model contained only one potential weather window, and for MaxT and rainfall, windows were defined to be at least one week long. We determined the time window that had the greatest association with chick mass as that with lowest AIC, and if this resulted in an improvement of $\Delta AIC > 5$ (a conservative threshold), we defined that time window as the ‘best’ time window. If no model resulted in an improvement of $\Delta AIC > 5$, we did not define a ‘best’ time window for that weather variable.

Critical windows can be defined either by ‘back-dating’ from the event of interest (in this case, date of chick weighing), or by calendar date with reference to a fixed time of year (see discussion in van de Pol & Cockburn, 2011). Preliminary analyses indicated a range of

effects at different times of year, which required a mixture of approaches. For events like the superb fairy-wren breeding season that occur across an extended period, short-term effects are likely to be more readily identified by back-dating (the weather in October will have different implications for nests in November than for nests in January). We therefore initially tested for associations by back-dating. However as this approach indicated changes in effects further back in the year (see below), and as conceptualising the timing of effects several months prior to an event is challenging compared to considering effects of weather at a given calendar date, we confined back-dating to a maximum of 100 days, and then also assessed long-term effects simply by calendar date (with day 1 defined as January 1 of a given year). This meant that the analyses of maximum temperature and rainfall were split into two stages: short-term effects estimated by back-dating, and longer-term effects estimated by calendar date.

We then fitted models of different weather variables sequentially, in order of closeness of windows to the time of measurement, with an expectation that heatwaves might have the most immediate effect. This meant a running order as follows: (i) immediate effects of heatwaves; short-term effects of (ii) maximum temperature and then (iii) rainfall (all three in time windows defined by backdating from measurement); and then long-term effects of (iv) maximum temperature and (v) rainfall (the last two in time windows defined by calendar date). In each case, the best windows identified in the previous models were also fitted as fixed effects: thus, for example, the model of long-term effects of MaxT also contained the heatwave index and the short-term effects of MaxT and rainfall. For max temperature and rainfall (both short and long term), we considered models in which the given index was fitted just as a linear effect, and then also as a quadratic function. Where the minimum AIC for the quadratic model was substantially better than the minimum AIC for the linear models

($\Delta\text{AIC} > 5$) for a given variable, we used the quadratic model (note that the linear vs quadratic models may not identify exactly the same best window: in practice, we found them to be not identical but very similar).

For graphical presentation of the associations between body mass and weather during windows defined by back-dating (for which there will necessarily be multiple values for a given year), we grouped observations into bins of 0.5°C (for temperature) or 10mm (for rainfall), and plotted the mean body mass within each bin. For windows defined by calendar date, we show annual values for the weather variable and annual mean body mass. In all figures, body mass was corrected for the variables in the initial model.

(ii) Identifying combined effects of multiple weather windows

Once we had identified the best critical window for each of the weather variables, we then determined the combination of weather variables with highest statistical support when considered in the same model (see for example Stopher *et al.*, 2014). Again, we used AIC for model comparison, and then estimated AIC weights for each model, defined as:

$$\text{AIC}_{\text{weight}} = \exp(-\Delta\text{AIC}/2) / \sum \exp(-\Delta\text{AIC}/2),$$

where the sum is across all models, and ΔAIC represents the difference in AIC between that model and the best (i.e. lowest AIC) model; AIC weights thereby indicate the relative support for each model.

Once we had identified a model containing the best time windows for all weather variables, we also checked for collinearity by dropping each in turn, to check that doing so did not change the other effects. We also tested for any two-way interactions between the different variables, and retained any significant interactions in a final model. For this final model, we

report ‘marginal’ and ‘conditional’ R^2 values, following (Nakagawa & Schielzeth, 2013), to represent the variance explained by just the fixed effects, and by both fixed and random effects, respectively. Finally, we checked for any trend in chick mass over time after having corrected for the weather effects, by adding year as a covariate to the final model.

Adding additional demographic parameters

As a final step, we tested the implications of adding further demographic parameters to the final model; these were not included in the earlier models to prevent mutual associations with weather variables obscuring any associations between weather and chick mass. In addition to year as a covariate, we added:

Female age: Age of the mother, defined as a three-level factor: one-year-old (25% of chicks), ‘older’ (older than one; 70%), and unknown (5%).

Number of helpers: the number of supernumerary males attending a nest, also treated as a three-level category of 0 (53% of chicks), 1 (28%) and 2+ (19%). As each territory will always have a dominant pair, the number of helpers also defines a ‘local’ population density of the number of birds on each territory.

Incubation date: the date on which incubation of a brood was initiated, in calendar days, fitted as a quadratic function. (There was no indication that timing of breeding had changed across the study period; LK and AC, unpubl. results.)

Population density: defined as the number of females breeding in a given year in the study area, corrected for the two-fold expansion of the study area in 1992.

Results

Temporal trends and initial model

Mean daily maximum temperatures across the whole year increased between 1988 and 2013 ($p < 0.001$; Figure 1a), as did the frequency of days with maximum temperature over 35° ($p < 0.001$, Figure 1b). There was no evidence of change in total rainfall ($p = 0.15$; Figure 1c), but this lack of association was strongly affected by an unusually wet year of 2010, without which the decline was significant ($p = 0.02$; Figure 1c, see legend for statistics).

Our initial model of chick mass without any weather variables (details in Supplementary Information (SI) Table S1) indicated that chicks put on an average of $0.91 (\pm 0.02\text{SE})$ g per day of age, an increase of 13% per day relative to the mean value of 7.01g on day 7, the median day of measurement. Males were on average $0.17 (\pm 0.02\text{SE})$ g heavier than females. There was no evidence in this initial model of a change in chick mass with increasing brood size ($-0.02\text{g} \pm 0.02\text{SE g}$ per extra chick). In a second model, after correcting for effects of chick age at measurement, sex, brood size and study sub-period, chick mass also showed no significant change over the study period (trend $= -0.00169 \pm 0.00450\text{SE g/yr}$; $p = 0.708$, Figure 1d).

We then used the sliding window approach to add weather variables to this initial model (but without year as a covariate). Below, we describe the best time window identified for each weather variable in turn, and then report a full model with all fitted together.

Short-term weather effects

Extreme heat events

There were significant effects of extreme heat (average maximum temperature across the window of $>35^{\circ}$) in a window spanning the two days prior to measurement, i.e. the day before measuring and the day before that. Although a total of only 2.4% of chicks in our sample experienced these two-day heatwaves, doing so was associated with a $0.39 (\pm 0.08\text{SE})$ g decrease in mean body mass (see the final model presented in Table 1).

Short-term maximum temperature effects

The best model for maximum temperature in a back-dating window indicated a positive effect of mean maximum temperature starting 25 days prior to measurement, and lasting for 19 days (i.e. running until 6 days prior to measurement). The mean value of this short-term index increased over the study period (Figure 2a; statistics in figure legend). In contrast to the adverse effects of heatwaves, chick mass initially increased with warmer temperatures; however the effect of temperature levelled off, which was reflected in the best model including a negative quadratic term (Table 1; Figure 2b).

Short term rainfall effects

Rainfall several weeks prior to weighing had a positive effect on chick mass, with the best window identified as starting 57 days earlier, and lasting for 44 days (Table 1; Figure 3b). There was no change in this weather index over the study period (Figure 3a), and there was no model improvement from including a quadratic term.

Long-term weather effects

Changing effects of weather across the year

Extending the period of back-dating considerably further back revealed surprising changes in the direction of the effects of maximum temperature. For illustration, Figure 4a shows the parameter estimates for models with 4-week windows of varying start date. Consistent with the results above, short term effects were positive; these were strongest for windows immediately prior to measurement, but significant effects persisted up to a window 147 days prior to banding. However, further back (150+ days) beyond that time point, the effects of temperature were consistently negative (Figure 4a).

Repeating the equivalent process for rainfall gave a hint of a similar change (positive effects in the short-term, some negative long-term effects), but one that was much reduced in magnitude (Figure 4b).

Long-term temperature effects

Backdating by time periods such as 150 days for an event which may occur any time between October and February becomes difficult to conceptualise. For longer term effects, we therefore switched to considering calendar days (see Methods). Doing so indicated a best model of a linear effect of average MaxT across a window running from calendar day 51 (21 February) to calendar day 68 (10 March), a period of 18 days inclusive. There was slightly stronger statistical support for a model with a quadratic effect, with a corresponding best window of day 52 to 63 (22 Feb to 5 March, 12 days inclusive); however the AIC difference between the best linear versus quadratic model was less than 5 ($\Delta\text{AIC} = 3.72$), so to be conservative given the multiple effects being tested, we used the linear model.

This long-term MaxT index did not increase over the study period (Figure 5a). However, the association between temperature in this period and chick mass in the subsequent breeding

season was negative (Figure 5b): an increase of 1°C early in the year resulted in chicks that were on average smaller by 0.052 (± 0.012 SE) g several months later (Table 1).

Long-term rainfall effects

None of the models of long-term effects of rainfall (defined by calendar day windows) resulted in a sufficient improvement ($\Delta AIC > 5$) to a model that already contained the short-term effects of all variables and the long-term effects of MaxT. We therefore only considered MaxT for long-term effects in the final model.

For all of the critical windows identified for the above weather variables, inspection of the AIC values showed similar support for other windows at approximately the same times (SI Fig. S2), implying that each was identifying robust effects of weather around those periods.

Final model

Final model with all weather variables

Comparison of models with different combinations of the above weather variables clearly indicated strongest support for a model containing all four weather terms (SI Table S2; $AIC_{\text{weight}} = 0.94$). This best model confirmed that maximum temperatures had three separate effects at different times of the year: an adverse effect of heat-waves in the preceding two days, a positive effect of temperature in the preceding weeks, and a very long-term negative association of temperature in the February and March preceding the relevant breeding season. The different weather effects were consistently independent of each other: in no case was the direction or significance of any effect dependent on the inclusion of any other variable in the model. We then tested for all two-way interactions between the possible combinations of

weather variables. The only significant interaction was a negative one between the short-term temperature and short-term rainfall indices (-2.72×10^{-4} (SE 1.04×10^{-4}), $p=0.009$), indicating that the effects of temperature were weaker at high rainfall levels, and vice versa (Suppl. Info. Figure 3). Table 1 shows the output of this final model, with all weather indices as identified above.

Finally, adding an additional variable of year to test for any temporal trend having corrected for all weather effects had no significant effect (parameter estimate = -1.14×10^{-3} (3.77×10^{-3} SE) g/year, $t=-0.303$, $p=0.764$).

Adding demographic parameters

The negative effects of the long-term temperature window are puzzling. We therefore tested whether they might be mediated through associations of temperature during this window with key demographic characteristics of the population, specifically age structure, group size (determined by the number of helpers) and population density, by adding these variables to the final model. We also included date of nest, with a quadratic term.

Age structure and helper number were both relevant for chick mass, though effect sizes were small: chicks of one-year-old mothers were 0.09 (± 0.03 SE) g lighter than those of older mothers, whereas those in nests with one helper were 0.13 (± 0.03 SE) g heavier on average, and those in nests with two or more helpers were 0.18 (± 0.04 SE) g heavier (SI Table S3). Incubation date had a quadratic effect, but there was no indication of any effect of population density estimated via the number of breeding females (SI Table S3). Again, there was also no indication of any trend over time.

More importantly, none of the demographic parameters or incubation date changed the effects of the weather variables (SI Table S3), giving no indication that any of the weather effects described above were mediated through associations with the other aspects of the population considered here. Furthermore, the effects of the demographic parameters did not change when the respective weather variables were dropped from the model in turn, again giving no indication of any collinearity between the weather variables and the demographic parameters.

Discussion

We present here an analysis of associations between climate and body size, specifically juvenile body mass – a trait that we know to be under strong viability selection, being positively correlated with the probability of juvenile survival in both sexes (LK and AC, unpubl. results). Our results show how effects of climate on body mass may vary within a population, between different times of year. Initial analyses showed changes in climatic variables (increased temperatures and frequency of heatwaves, and an indication of reduced rainfall), but no apparent change in the mass of superb fairy-wren chicks. Superficially, this would suggest a lack of a plastic response of chick mass to weather. The more detailed analyses revealed a complex set of associations with different components of weather, including to our knowledge the first report of effects of the same weather variable (maximum temperature) at different times of year having contrasting associations with body size at a later time of year. Below, we discuss effects of each weather variable briefly, dealing with the relatively more straightforward effects of rainfall first, and then consider the implications of such patterns for analyses of the effects of climate change on wild animal populations.

Biological explanations for effects in superb fairy-wrens

Our results indicated positive effects of rainfall across an approximately six-week period starting eight weeks prior to chick measurement. Higher rainfall during late spring and early summer will presumably enhance vegetation growth and thereby increase insect abundance (e.g. Frith & Frith, 1985; Lowman, 1982; Woinarski & Cullen, 1984); this will increase the availability of food to be provided to chicks, which are fed almost exclusively on invertebrates. The timing of the best critical window identified here, ceasing just under a fortnight before chick measurement (and so a week prior to hatching), fits with a reasonable expectation of the timing of response of first vegetation and then arthropod abundance. Thus, rainfall up to and during the breeding season may reflect protein availability for growing chicks. In further support of rainfall being a limiting factor in this population, higher rainfall in the spring leads to sharply increased reproductive success (number of young reared to independence: Cockburn et al 2008b) and higher rainfall through the previous summer and autumn is associated with early dates of males moulting into breeding plumage, although over a longer time window than here (Cockburn *et al.*, 2008a; van de Pol *et al.*, 2011).

Temperature associations were more complex. The occurrence of two days of temperatures above an average of 35°C reduced chick mass by 0.3g – equivalent to a third of a day's mass gain. We cannot be sure if this was a direct effect due to dehydration or lethargy of chicks, or an indirect result of reduced foraging or provisioning effort by parents or helpers facing heat stress; it is likely to be both. These heatwaves were rare, mainly because their frequency was highest in January after the peak of the breeding season (see SI Fig. S1 for seasonal change in temperature; a total of only 2.4% of chicks in the sample experienced a 2-day heatwave), and they are therefore currently unlikely to be having major effects on population dynamics via any impact on chick body size. Nevertheless, the effect illustrates the potential for extreme

weather events to impact growth even in temperate regions, and adds to other evidence of heatwaves having sub-lethal but nonetheless adverse effects on wild animal populations. For example, temperatures above critical thresholds reduce growth rates of common fiscal (*Lanius collaris*) chicks (Cunningham *et al.*, 2013b), and mass gain in southern pied babblers (*Turdoides bicolor*, du Plessis *et al.*, 2012).

Maximum temperatures at longer intervals prior to the nestling period were associated with chick mass in contrasting ways. Over the shorter term, increased temperatures in the weeks immediately prior to the nesting period were associated with heavier chicks; the interaction term indicated that this was especially so when the rainfall in the preceding weeks had been relatively low (SI Figure S3). As with rainfall, the positive relationship may be driven by increased arthropod abundance at warmer temperatures (e.g. Lowman, 1982; Woinarski & Cullen, 1984) – especially as 82% of chicks are weighed prior to 31st Dec, i.e. at a time of year earlier than the stronger heat of January (SI Fig. S1). Alternatively, or possibly additionally, effects of warmer temperatures may be acting through a reduced need for brooding by the mother for younger chicks, and/or for investment in thermoregulation by older chicks (Gillooly *et al.*, 2001). Such effects are likely to be most severe during cooler periods early in the breeding season, and it is notable that the positive effects of an increase in maximum temperature were only relevant at below-average temperatures (Figure 2).

An explanation for the long-term adverse effects of higher maximum temperatures in the February and March preceding a breeding season that starts many months later is more difficult. We discovered this long-term window through our analytical method, rather than predicting its occurrence *a priori*. Nevertheless, the time identified is biologically significant for a variety of reasons. First, at this time females will usually have just ended a very long

breeding season. Second, during late January and early February many young females leave their natal territory and settle on a foreign territory in order to overwinter (Cockburn *et al.*, 2003). Finally, it is during this period that old males in good condition may renew their nuptial plumage and continue to court extra-group mates, rather than moulting into an eclipse plumage for the winter (Cockburn *et al.*, 2008a). It is hence a time when major reproductive decisions are made and when population density is at its highest – and hence which may be important for determining maternal (or paternal, or helper) effects on offspring in the subsequent breeding season.

However, possible consequences of these aspects were not strongly supported. Associations between the long-term temperature index and chick mass were not mediated by any other life history or demographic parameters, such as a changing age structure amongst mothers, or variation in the numbers of helpers at the nest: both variables affected chick mass, but not in any way that altered the associations with any of the climatic indices. We also did not find any effect of any measure of population density, via either very local population density (which would be reflected in an effect of helper number) or overall population density (estimated via number of breeding females; results were equivalent for male numbers). The Supplementary Information describes further analyses of other potentially relevant variables, but again these did not indicate a clear mechanism by which the long-term association might be acting. Thus one of the most plausible explanations for the long-term temperature association in Figures 4 and 5 remains an adverse impact of higher temperatures on condition of parents (or helpers) at a high-density, relatively hot time of year, which carries over to impact on egg size or composition, and possibly even chick provisioning, in the subsequent breeding season. Maternal (or ‘carer’) effects of this type would be in line with observations of effects of maternal condition prior to breeding on offspring performance generally (e.g.

Gorman & Nager, 2004; Martin, 1987). As an additional, not necessarily exclusive, explanation, there may also be long-term adverse effects of the hotter temperatures at this time on either vegetation and/or arthropod productivity later in the year, especially as February-March is a period at which insect numbers drop from mid-summer peaks in SE Australian forests (e.g. Frith & Frith, 1985; Lowman, 1982). However at present we are unable to pin this down further.

Implications for studies of effects of climate change

The contrasting effects of immediate, short- and long-term effects of temperature on chick mass constitute, to our knowledge, rare evidence of within-population differences between associations of temperature at different times of year with a morphological trait measured at a later time. The results are similar to a detailed analysis of growth at different ages in common fiscal nestlings in the Kalahari, which showed reversals in the effects of maximum temperature on a given day on chick mass and tarsus length: higher temperatures in the first few days of the nestling period promote growth, but reduce it during later days (39 chicks in 13 broods, Cunningham *et al.*, 2013b). Analyses of 23 years of data from another Australian passerine, the white-plumed honey-eater *Ptilotula (Lichenostomus) penicillatus*, found positive associations between different aspects of temperature (also including occurrence of heatwaves) and body mass, but also indicated a complex web of associations that vary across time-scales and age classes (Gardner *et al.*, 2014b). Such fine-scale variation, showing changes in effects of temperature in different seasons or at different ages, underlines the value of detailed individual-level analyses in exploring climate change effects on body size. Contrasting effects of temperature at different times of year can also generate divergent responses in plant phenology: although warming spring temperatures will accelerate timing

of flowering, warming autumn/winter temperatures will delay it, possibly due to the plants' requirement for prolonged winter chilling to be able to flower the subsequent spring ('vernalization', see e.g. Cook *et al.*, 2012; Luedeling *et al.*, 2013; Roberts *et al.*, 2015). Such results further illustrate the little-understood complexity in biotic responses to climate warming.

What are the implications of the effects observed here for body size dynamics in this population, given predictions for future climate change? Overall, the climate in south-eastern Australia is expected to become warmer and drier (I.P.C.C., 2013), a scenario which might be expected to result in a decrease in chick mass given the adverse implications via rainfall, heatwaves and long-term temperature. However, any such calculations would clearly be overly simplistic were they to assume that each weather variable would change in the same way. Our analyses have shown that despite clear patterns at the annual level (Figure 1), weather during the specific relevant windows of the year may show little or no change: here, although the frequency of heatwaves and the short-term temperature index both increased over our study period (Figs 1b and 2a), neither the rainfall index nor the long-term temperature index changed (Figs 3a and 5a). Thus considering the observed changes in weather within the relevant time windows, we would expect negligible changes in chick mass due to either the rainfall or the long-term temperature effect, a decrease of 0.01g due to increased frequency of heatwaves, and an increase of 0.05g due to the observed increase of 2.1°C in the mean of the short-term temperature index, resulting in a net increase of 0.04g across the study period – a value that lies with the confidence interval on the observed change in body mass over the 26 years (Figure 1d). These changes are clearly all very small in magnitude relative to the mean body size of 7.07 (± 1.04 SD) g, and illustrate the general point that sensitivity to weather may still not result in a temporal trend even in a rapidly

changing climate; small changes such as these are highly unlikely to have major implications for survival or fecundity. This is a qualitatively different conclusion from what might have been expected under a simple assumption of a general shift to warmer and drier conditions. It also argues against concluding that an observed association between weather at a given time point and morphology implies adverse effects of climate change on a population, highlighting the value of more comprehensive analyses.

Although we have strong statistical support for the significance of all of the different weather variables, and although each is associated with clear effects on mean chick mass (Figs. 2, 3 and 5), the year-to-year variation in chick mass relative to other sources is small: in the initial model prior to the introduction of the weather variables, cohort effects comprise 2.2% of the total variation (SI Table S1). The inclusion of weather variables explained approximately half of this inter-annual variation (remaining cohort effects were reduced to 1.1% of variation, Table 1), but this proportion is still small compared, for example, to differences between broods, which will be driven by within-season variation (of which a substantial portion may be due to within-season weather changes), genetic effects, maternal effects, reproductive history and so forth. Similarly, the marginal R^2 (Nakagawa & Schielzeth, 2013) of a model excluding weather effects is only 2.4% lower. In a similar fashion, Salewski et al. (2013) report analyses of effects of multiple weather variables on survival of 7 European passerine species, in which weather variables explained an average of 5% of total variation in survival. Thus whilst understanding effects on natural populations of year-to-year variation due to a changing climate is a primary aim for many current ecological studies, evaluation of their importance relative to other sources of variation is worthwhile, and the current active interest in quantifying long-term trends in body size should also bear in mind their magnitude and

likely ecological significance, rather than simply focusing on their statistical significance (Gardner *et al.*, 2011; Yom-Tov & Geffen, 2011).

Our analyses of the influence of weather revealed effects that were linear, quadratic, based on a threshold, and due to interactions between two different weather variables; they also indicated multiple different times of year at which weather was relevant. Such complexity is perhaps not surprising, but it requires careful analysis. Here, a sliding window approach provided the simplest means of dissecting this cocktail of effects. We initially ran analyses using more complex functions that differentially weighted past weather according to specific functions such as a Weibull function, using an approach which was suggested and successfully used to describe variation in the male plumage phenology in this same study system (van de Pol & Cockburn, 2011). However for analyses of chick mass, we found that results from these models were heavily dependent on the starting values used, in ways that became too subjective to comfortably allow robust inference. This observation supports the authors' recommendations to explore a range of starting values when implementing the methods (see code in appendix of van de Pol & Cockburn, 2011). It also illustrates how, in some cases – as for example here, where multiple peaks are involved – a simpler approach may be required. Furthermore, even where a simpler approach such as a sliding window is used, the practice to date has typically been to identify a single 'best' window for a given weather variable (e.g. Husby *et al.*, 2010; Stopher *et al.*, 2014), and use that in subsequent analyses. Our results indicate that evaluating the potentially varying effects of weather at different times of year (Fig. 4) and allowing for potentially multiple effects of the same variable, is informative (see also Gardner *et al.*, 2014b). Furthermore, because associations at unexpected times of year may appear, analyses should not be too heavily restricted by *a priori* expectations. Most sobering of all, analyses of phenotypic plasticity or genotype-

environment interactions typically require a single environmental predictor for the x-axis of individual reaction norms (Gienapp & Brommer, 2014; Nussey *et al.*, 2007). The complexity found here implies that such analyses would be a daunting prospect.

Our results illustrate the importance of considering the full annual cycle of a species in studies of a population's response to climate change. The scenario presented here illustrates that: (i) there may be no temporal trend in a phenotypic trait despite it being sensitive to changing weather; (ii) a trait that occurs at one time of year may depend on both short and long-term effects of climate at different times of year; (iii) these effects may be in different directions: warmer temperatures may have adverse effects at some times of year (here, during a warmer period) but beneficial effects at others (here, during a cooler period). In addition, (iv) the relevant climatic variables may change at different rates. We can also infer that (v) as climate changes, there will be the potential for sensitivity either to increase, with greater experience of relevant events (e.g. heatwaves), or to decrease as they are experienced less (e.g. the short-term effect of lower temperatures). All five points illustrate the complexity that may underlie associations between climate and phenotypic traits. Finally, population-level effects of weather may be relatively small compared to larger-scale variation at the level of the individual or brood. Much work on identifying effects of weather is motivated by the hope of predicting the consequences of future climate change. In a system such as this, attempting to do so may be unrealistically ambitious, requiring identification of all relevant time periods at which weather is important plus understanding of how the weather within those periods will change. Further ambitions of determining the implications for population dynamics may then become entirely unrealistic. It will therefore be important to determine how general the complexity of patterns observed here is across other traits and other systems.

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Supporting Information Legends

Supporting Information (SI) Tables S1-S3 and Figures S1-S3.

Tables

Table 1. Mixed model of chick mass, including main effects of ‘best’ windows for weather variables at different times of year. Heatwave: mean MaxT > 35°C in two days prior to measurement; MaxT short-term: window starting 25 days prior to measurement and lasting for 19 days; Rainfall short-term, window starting 57 days prior to measurement and lasting 44 days; MaxT long-term: window running from 21 Feb to 10 March each year. All continuous variables were mean standardised. N = 6405 chicks, 2309 broods, 26 cohorts.

<i>Fixed effects</i>	<i>Parameter estimate</i>	<i>SE</i>	<i>T</i>	<i>p-value</i>
Intercept	7.332	0.091		
Chick age (days): linear	0.908	0.017	52.377	<0.001
quadratic	-0.079	0.021	-3.846	<0.001
Sex (relative to fem.): male	0.165	0.016	10.335	<0.001
: unknown	0.045	0.036	1.250	0.212
Brood size	-0.038	0.017	-2.314	0.020
Study sub-period (effect of pre-1992)	0.761	0.068	11.112	<0.001
Two-day heatwave	-0.372	0.084	-4.426	<0.001
MaxT short-term : linear	2.21×10^{-2}	-0.37×10^{-2}	5.846	<0.001
: quadratic	-0.31×10^{-2}	-0.09×10^{-2}	-3.285	0.001
Rainfall short-term	-1.47×10^{-3}	-0.32×10^{-3}	4.621	0.002
MaxT long-term	-0.051	0.012	-4.105	<0.001
MaxT short-term * Rainfall short-term interaction	-3.07×10^{-4}	0.98×10^{-4}	-3.138	0.002
<i>Random effects</i>	<i>Variance component</i>			
Brood identity	0.271			
Cohort	0.006			
Residual	0.245			
<i>Model AIC = 12394.9</i>				
<i>Marginal $R^2 = 0.498$</i>				
<i>Conditional $R^2 = 0.764$</i>				

Figure legends

Figure 1. Temporal trends in (a-c) annual weather and (d) chick body mass across $n=26$ years: (a) annual mean maximum temperature (slope= $0.072 \pm 0.018\text{SE } ^\circ\text{C/yr}$, $t_{24} = 4.004$, $p<0.001$); (b) the number of single days $>35^\circ\text{C}$ per year (slope = 0.30 ± 0.12 , $t_{24}=2.46$, $p=0.021$); (c) total rainfall per year (slope= $-5.35 \pm 3.61\text{SE mm/yr}$, $t_{24} = -1.482$, $p=0.151$; excluding 2010, slope = $-7.80 \pm 3.24\text{SE mm/yr}$, $t_{24} = -2.41$, $p=0.024$: the regression line shown in the figure includes 2010); (d) mean chick mass (from mixed model of individual-level data, correcting for other fixed effects as described in Methods; slope= $-0.0017 \pm 0.0045\text{SE}$; $t_{24} = -0.377$, $p=0.708$). Dotted lines are 95% confidence intervals.

Figure 2. Changes in (a) annual mean short-term MaxT index : mean value each year across climate window starting 25 days prior to banding and running for 19 days (increase over time = $0.086 \pm 0.030 ^\circ\text{C/yr}$, $t_{24}= 2.855$, $p=0.009$); (b) Mean chick mass (corrected for other fixed effects, see Methods) in relation to MaxT index (data grouped into bins of 0.5°C , with all values $>32^\circ$ combined). Solid lines show regressions fitted through points shown (quadratic for (b)); dotted lines are 95% CIs.

Figure 3. Changes in (a) short-term rainfall index (mm): mean value each year across climate window starting 57 days prior to banding and running for 44 days, averaged across all nests in a given year (slope = $-0.045 \pm 0.909 \text{ mm/yr}$, $t_{24}= -0.050$, $p=0.961$); (b) mean chick mass (corrected for other fixed effects, see Methods) in relation to rainfall index (grouped into bins of 10mm, with all values over 210mm combined into a single bin). Solid lines shows regressions fitted through points shown; dotted lines are 95% CIs.

Figure 4. Effect of weather in 4-week windows at different time points earlier in the year.

The y-axis shows the parameter estimate from a model with a window starting at a varying number of days (shown on x-axis; points are at weekly intervals) prior to chicks being weighed, with error bars showing two SEs of the parameter estimate. Parameter estimates are for (a) mean MaxT and (b) total Rainfall.

Figure 5. Changes in (a) long-term MaxT index (the mean value of MaxT in °C between 21 Feb and 10 March; regression line slope = -0.0351 ± 0.0486 °C/yr, $t_{24}=-0.722$, $p=0.477$) over the study period; (b) annual mean chick mass (corrected for other fixed effects, see Methods) in relation to long-term MaxT index that year (in °C); regression line fitted through points shown. Dotted lines are 95% CIs.

Supplementary Information

Contrasting effects of climate on juvenile body size in a Southern-hemisphere passerine bird

Loeske E. B. Kruuk, Helen L. Osmond and Andrew Cockburn

Supplementary Tables

1. Supplementary Table S1.

Initial linear mixed model of chick mass (in g), describing effects of chick age, sex, brood size and sub-period, before considering weather variables. Chick age and brood size are both mean standardised. N = 6405 chicks, 2309 broods, 26 cohorts. Chicks of unknown sex are closer in their mean value to females because of the likely higher frequency of females amongst them (chicks cannot be sexed phenotypically in the nest, so information on sex relies either on their having been genotyped, and/or being seen later in life: the latter is more likely for males, given their philopatry).

<i>Fixed effects</i>	<i>Parameter estimate</i>	<i>SE</i>	<i>t-statistic</i>	<i>p-value</i>
(Intercept)	6.926	0.031		
Chick age (days): linear	0.908	0.018	51.420	<0.001
quadratic	-0.071	0.021	-3.390	<0.001
Sex (relative to female): male	0.168	0.016	10.510	<0.001
: unknown	0.058	0.037	1.550	0.122
Brood size	-0.017	0.017	-1.030	0.302
Study sub-period (effect of pre 1992)	0.627	0.077	8.160	<0.001
<i>Random effects</i>	<i>Variance component</i>	<i>LRT</i>	<i>p-value</i>	
Brood identity	0.288	1632.9	<0.001	
Cohort	0.012	36.84	<0.001	
Residual	0.245			
<i>Model AIC = 12495.14</i>				
<i>Marginal R² = 0.474</i>				
<i>Conditional R² = 0.764</i>				

2. Supplementary Table S2.

Comparison of the six highest-ranking models for effects of weather variables on chick mass. 'Heatwave' = whether average MaxT in the 2-day period prior to measuring exceeded 35 °C; 'MaxT.ST' = short-term effects of mean maximum temperature across window starting 25 days prior to measurement, running for 19 days (and its quadratic, 'MaxT.ST²'); 'Rain.ST' = short-term effects of total rainfall in window starting 57 days prior to measurement, running for 44 days; 'MaxT.LT' = long-term effects of mean maximum temperature across window running from 21 Feb to 10 March. ΔAIC is the difference from the top model, containing all terms; AIC-weight is as defined in the Methods.

Model	AIC	ΔAIC	AIC-weight
Heatwave+MaxT.ST+MaxT.ST ² +Rain.ST+MaxT.LT	12402.73	0	0.935
Heatwave+MaxT.ST+Rain.ST+MaxT.LT	12408.20	5.47	0.061
Heatwave+MaxT.ST+MaxT.ST ² +Rain.ST	12413.66	10.93	0.004
Heatwave+MaxT.ST+MaxT.ST ² +MaxT.LT	12416.97	14.24	0.001
MaxT.ST+MaxT.ST ² +Rain.ST+MaxT.LT	12421.53	18.80	0.000
Heatwave+Rain.ST+MaxT.LT	12456.87	54.14	0.000

3. Supplementary Table S3.

Mixed model of chick mass including additional demographic variables as well as best windows for weather variables at different times of year. Additional variables: number of helpers (category 0, 1 or 2+); mother's age (older (2+), one year old, or unknown); incubation date and its quadratic, and density of breeding females. All continuous variables were mean standardised. Definitions of weather variables are given in legend for Suppl. Table 2.

N = 6113 chicks, 2197 broods, 25 cohorts (sample sizes are slightly reduced compared to Table 1 because of missing data on some of the additional variables included here).

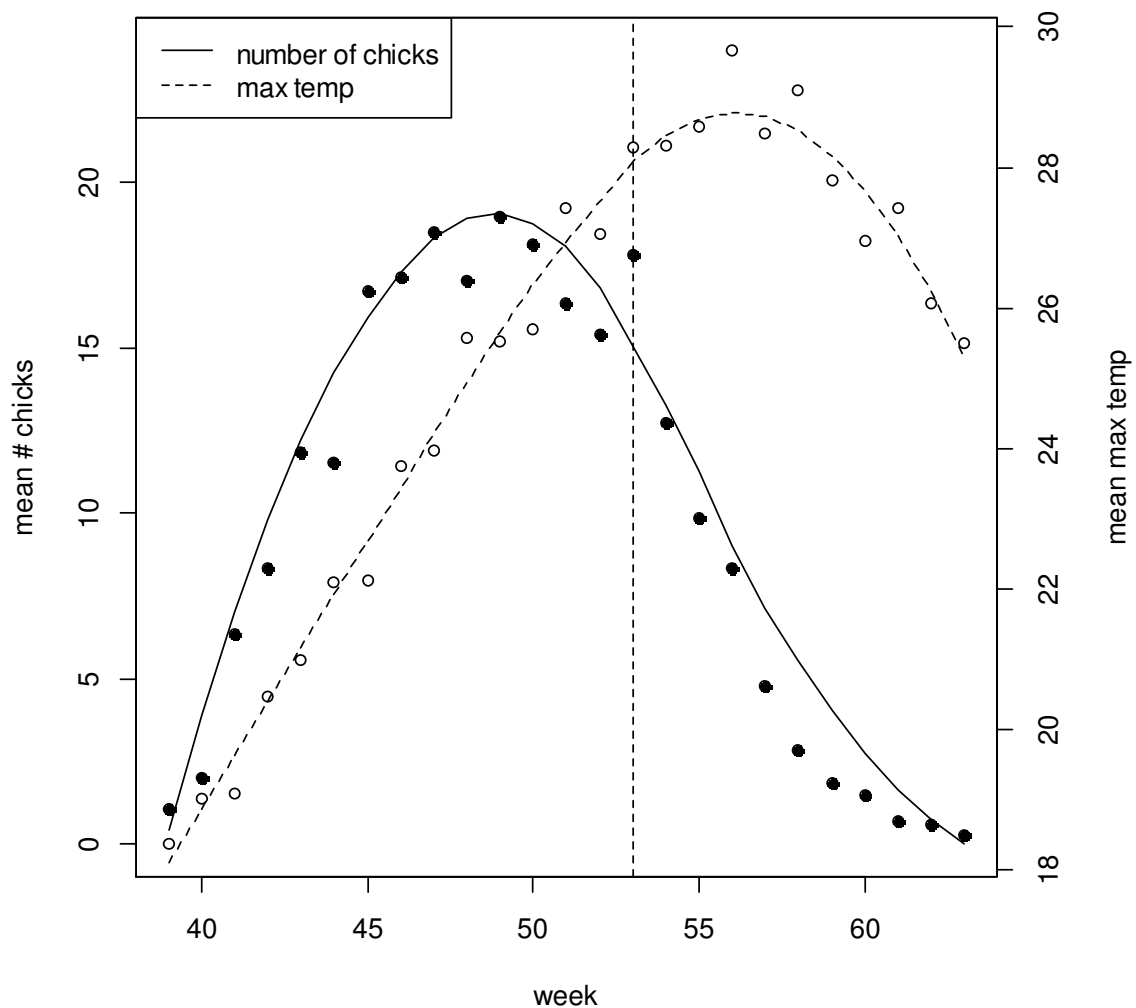
<i>Fixed effects</i>	<i>Parameter estimate</i>	<i>SE</i>	<i>t-statistic</i>	<i>p-value</i>
(Intercept)	7.273	0.093		
Chick age (days): linear	0.925	0.018	50.722	<0.001
quadratic	-0.081	0.021	-3.759	<0.001
Sex (relative to female): male	0.166	0.016	10.395	<0.001
: unknown	0.054	0.040	1.364	<0.001
Brood size	-0.051	0.018	-2.848	0.004
Study sub-period (effect of pre 1992)	0.717	0.086	8.300	<0.001
# helpers (relative to 0) : 1	0.123	0.031	4.017	<0.001
2+	0.175	0.036	4.854	<0.001
Mum age (relative to Older): 1 yr old	-0.084	0.031	-2.692	0.007
Unknown	0.121	0.072	1.691	0.090
Incubation date: linear	-1.429 x 10 ⁻³	0.870 x 10 ⁻³	-1.642	0.101
: quadratic	-1.208 x 10 ⁻⁵	1.349 x 10 ⁻⁵	-0.896	0.370
Density of breeding females	-3.113 x 10 ⁻³	0.002	-1.353	0.187
Two-day heatwave	-0.354	0.085	-4.176	<0.001
MaxT short-term: linear	3.379 x 10 ⁻²	0.766 x 10 ⁻²	4.413	<0.001
: quadratic	-0.318 x 10 ⁻²	0.107 x 10 ⁻²	-2.980	0.003
Rainfall short-term	1.776 x 10 ⁻³	0.351 x 10 ⁻³	5.059	<0.001
MaxT long-term	-0.055	0.012	-4.525	<0.001
MaxT short-term * Rainfall interaction	-3.095 x 10 ⁻⁴	1.038 x 10 ⁻⁴	-3.005	0.003
Year	-2.289 x 10 ⁻³	4.025 x 10 ⁻³	-0.706	0.573
<i>Random effects</i>				
Brood identity	0.268			
Cohort	0.005			
Residual	0.243			
<i>Model AIC = 11785.28</i> <i>Marginal R² = 0.507</i> <i>Conditional R² = 0.768</i>				

In further analyses (not shown), we also tested for effects of timing of breeding, both in relation to when a female finished breeding in the previous season (i.e. just prior to the long-term MaxT window), or timing of her initiating breeding in the current season, but again the weather-mass association was robust to inclusion of these variables. There was also no indication of any difference in the association for chicks with one-year-old (i.e. fledged in the previous year) versus older mothers, which we had anticipated might be the case were the association to be driven by carry-over costs of reproduction on adults from the previous year. Finally, we also considered the possibility that the *range* of temperature experienced during the day (rather than the maximum) might be relevant, but in the equivalent analyses, temperature range was less informative than maximum temperature, and was never significant in a model that already contained maximum temperature.

Supplementary Figures

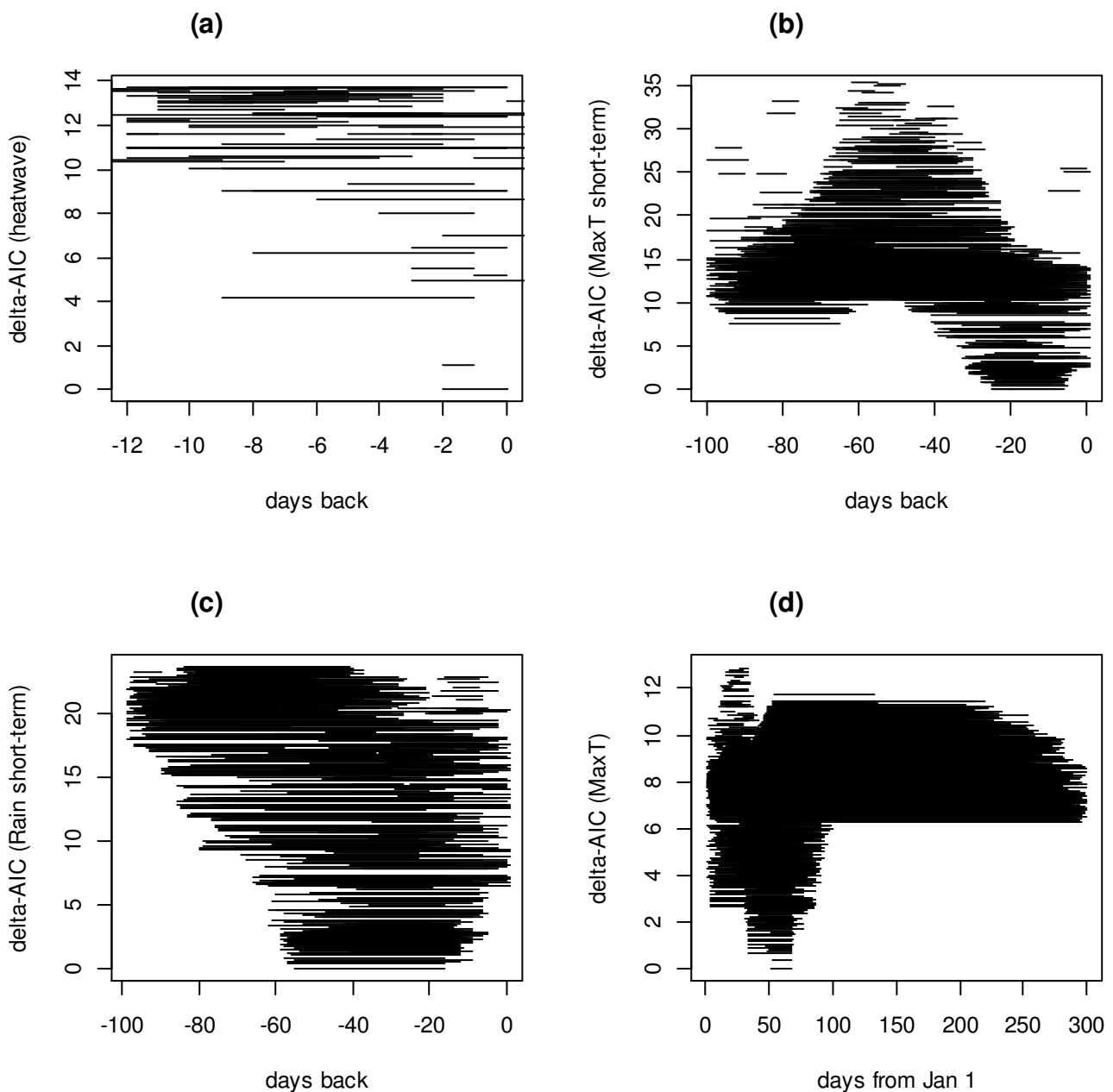
4. Supplementary Figure S1.

Time at which chicks were present through a season. Week 1 = from January 1st; week 53 (dashed vertical line) = January 1st in next calendar year. Left-hand axis: annual mean number of chicks banded per week; right-hand axis: mean maximum temperature during that week, averaged across all years.



5. Supplementary Figure 2.

Comparison of AIC values for models testing the effect of weather variables over different critical windows on chick mass. Y-axis shows ΔAIC (delta-AIC), the difference between the best model (that with lowest AIC) and a model with a window defined by the window shown; the best windows therefore correspond to $\Delta\text{AIC}=0$. Each model contained only one window, but some models may have the same AIC and hence apparently long windows may in fact contain multiple overlapping windows. Values are shown for models of: (a) immediate effects of heatwaves: whether or not the average temperature over the window exceeded 35°C ; (b) maximum temperature in the short term (with windows defined by number of days prior to chick measurement, up to a maximum of 100 days); (c) rainfall in the short term; (d) maximum temperature over the year prior to the breeding season (with windows defined by calendar date, starting Jan. 1).



6. Supplementary Figure 3.

Predicted effect on chick mass of the interaction between the short-term (ST) maximum temperature index and the short-term rainfall index (see Supplementary Table 2 legend for details of the respective windows). Parameter estimates are taken from the model in Table 1.

